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The world's highest vascular epiphytes found in the Peruvian Andes

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Abstract The highest elevation epiphytic vascular plant flora ever recorded on a worldwide basis is described from the Cordillera Vilcabamba, southern Peruvian Andes. Three species of fern (*Melpomene*, *Polypodium*: Polypodiaceae) were recorded from *Polylepis pepeii* forests at elevations above 4,250 m, with *Melpomene peruviana* reaching almost 4,550 m. A new high-elevation world record for arboreal hemiparasites is also documented, with *Tristerix longebracteatus* (Loranthaceae) being found at c.4,620 m. Climatic conditions of these sites were assessed and are discussed in the light of existing hypotheses on the abiotic conditions limiting epiphytism.

Keywords Arboreal hemiparasites · *Polylepis* · *Melpomene* · Polypodiaceae · Loranthaceae

Introduction

Vascular epiphytes include close to 28,000 species, corresponding to roughly 9 % of the world's vascular plant flora (Zotz 2013a). They are, by definition, higher plants with vascular tissue (xylem and phloem) that grow on other plants, but obtain their nutrients and water entirely from the

atmosphere and organic layers on the branches or trunks of their host plants. Epiphyte diversity is highest in humid tropical cloud forests at about 1,000–2,000 m elevation (Cleef et al. 1984; Wolf 1994; Hietz and Hietz-Seifert 1995; Muñoz and Küper 2001; Wolf and Flamenco-S 2003; Bhattarai et al. 2004; Küper et al. 2004; Krömer et al. 2005). This presumably reflects the optimal living conditions for epiphytes, whose growth is limited by light, water and nutrient availability and low temperatures (Benzing 1990). Despite these limitations, vascular epiphytes have also conquered extreme environments ranging from dry semi-deserts (Garcia-Suarez et al. 2003) to cold boreal forests at high latitudes (Maycock 1975; Zotz 2002; Zotz and List 2003).

In mountains, little is known about the upper limits of vascular epiphytic growth. In the northern hemisphere, only two studies in the Himalayas have found epiphytic ferns above 3,500 m (Mehra and Vij 1974) and reaching to 4,000 m (Bhattarai et al. 2004). In the southern hemisphere, high-elevation grammitid fern epiphytes have been recorded from *Polylepis* (Rosaceae) forests in the Andes of South America to 4,000 m in Bolivia (Krömer et al. 2005) and 4,300 m in Ecuador (Lehnert 2013).

Albeit not considered epiphytes, arboreal hemiparasites can also form important components of the canopy in montane forests. All previous records of high-elevation arboreal hemiparasites pertain to the mistletoe family Loranthaceae (2,800 m in the Himalaya, Devkota et al. 2010; 1,250 m in Europe, Dobbartin et al. 2005) with the highest elevational record held by a number of *Tristerix* species from Peru documented at 4,000–4,500 m (Brako and Zarucchi 1993). All members of Loranthaceae form direct contacts with their hosts by means of haustoria, but those which are hemiparasitic also have chlorophyllous leaves which allow them to photosynthesise.

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There is a paucity of information regarding the abiotic conditions that limit epiphytism in temperate zones (Zotz 2003) with it being generally believed that frost occurrence and moisture availability are the key limitations (Zotz 2005). When considering the differences in vascular epiphyte diversity with elevation, temperature (in particular the regular occurrence of frost) has been advocated as the principal limiting factor on vascular epiphytism at higher elevations, but the mechanisms involved are still unknown (Gentry and Dodson 1987; Kessler 2001a, b; Bhattarai et al. 2004; Kreft et al. 2004; Krömer et al. 2005). The elevational limits of arboreal hemiparasitic mistletoes are suggested to be governed, not only by climatic factors, but also by the abundance and availability of avian dispersers (Devkota and Acharya 1996; Ladley and Kelley 1996). Cold and moist habitats found at higher elevations are generally avoided by mistletoe-associated birds leading to a lack of dispersal to these habitats.

At high elevations in the tropics, a further limitation on both epiphyte and arboreal hemiparasite occurrence is the lack of suitable substrate, i.e. the lack of trees at high elevations. The vast majority of high-elevation treeline positions, especially in tropical mountains with their long history of human habitation, have been depressed by at least several hundred metres due to logging, cattle grazing and burning with natural treeline relicts only found as isolated stands in difficult to access areas (Kessler 1995a). This poor accessibility has hindered research on these high-elevation treeline environments.

Polylepis forests are excellent candidates for hosting the world record for high-elevation vascular epiphytes as they are considered to be the world's highest treeline with trees reaching to 4,900 m (Kessler et al. 2014). Our recent exploration in the humid Cordillera Vilcabamba of southern Peru has found *Polylepis pepeii* forests reaching much higher elevations than previously documented (Simpson 1979; Kessler 1995b), with forests being found to 4,650 m. These forests host a diverse epiphyte flora including a number of grammitid fern species.

In all previous studies examining vascular epiphytism with relation to elevation, none have reached the absolute elevational limits of epiphytism or studied the abiotic conditions under which these epiphytes can survive. Our study, thus, not only provides a new world record for high-elevation vascular epiphytes, but also insight into the abiotic constraints of epiphytism at their ecophysiological limits.

Material and methods

Sites and study area

The study was conducted in the high mountain areas of the Cordillera Vilcabamba, Province of La Convención, Cusco

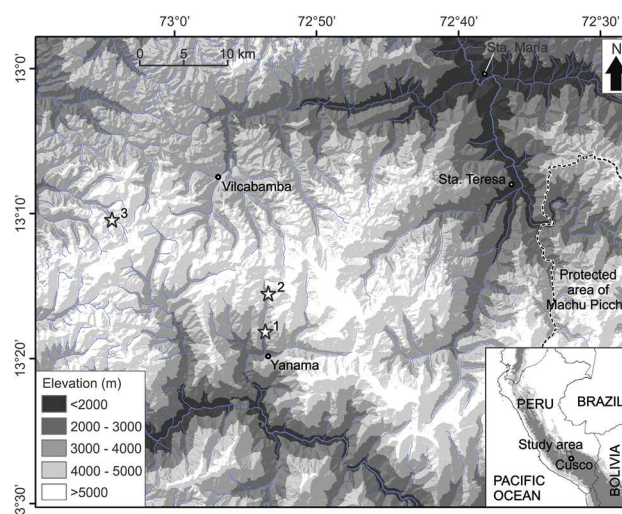


Fig. 1 Map of the study area showing the three study sites (denoted by numbered stars). ASTER DEM raster map provided by METI and NASA Land Processes Distributed Active Archive Center

region, in the southern Peruvian Andes ($S13^{\circ} 10'$, $W73^{\circ} 03'$, $>4,250$ m). The climate of the area is relatively humid from receiving updrafts of humid air from the Amazon basin, and there is a clear wet season from November to April. Diurnal temperature fluctuations are very pronounced, especially in the dry season. The vegetation of the study region contains floristic elements of both the humid páramo, found in northern Peru (Marcelo-Peña et al. 2006; Tovar et al. 2012), and the dry puna, which occupies the majority of the high-elevation landscapes of central and southern Peru (Wilcox et al. 1986, 1987; Florez-Martínez 2005).

Three sites, which were comprised of *Polylepis pepeii* forests found at their upper elevational limits, were studied within the Cordillera Vilcabamba (Fig. 1 and ESM). Site 1 was located within the highest forest found on the north side of the lower Phacchaq valley, 4 km north of Yanama, district of Santa Teresa ($S13^{\circ} 17' 02.0''$ $W72^{\circ} 50' 02.6''$, 4,200–4,650 m). Site 2 was located within the forested mountain ledges on the uppermost eastern portion of the Phacchaq valley, 8.5 km north of Yanama, district of Santa Teresa ($S13^{\circ} 15' 16.9''$ $W72^{\circ} 50' 22.5''$, 4,250–4,490 m). Site 3 was located on the forested large prominent ledge on the south facing cliff at the end of the Totorá-Purkay valley, 4 km east of the Totorá-Purkay village, district of Vilcabamba ($S13^{\circ} 11' 00.2''$ $W73^{\circ} 03' 07.6''$, 4,400–4,550 m).

Data collection

Voucher specimens of the epiphytes encountered were collected and identified in the herbarium and are deposited at the herbaria CUZ, LPB, STU and Z. Plant nomenclature follows W3TROPICOS (Solomon 1999). Elevation was measured using a Garmin Etrex H handheld GPS device

which was tested at landmarks with documented elevations and found to have a precision of ± 10 m.

Relative air humidity and temperature were recorded using digital dataloggers (DS1923 Hygrochron iButtons; Hubbart et al. 2005). Dataloggers were placed at sites 1 and 2 (Fig. 1, ESM), on a field trip in May 2012. The datalogger at site 1 was placed at c. 4,566 m (S13° 17' 01.4" W72° 50' 01.5"), whilst the datalogger at site 2 was placed at c. 4,494 m (S13° 15' 13.8" W72° 50' 24.0"). The elevational difference of c.72 m between sites was deemed to have little or no effect in explaining the differences in climate exhibited at each site. The dataloggers were placed on raised platforms 20 cm from the ground surface. These platforms were shielded from direct sunlight and rain and were located close to where the epiphytes were encountered. Dataloggers were placed at either c.40 or c.20 m distance and either c.40 or c.3 m higher elevation than the highest epiphyte specimens encountered at sites 1 and 2, respectively. These differences in elevation and distance of the dataloggers from the highest epiphytes encountered were not deemed significant and so the climatic variables recorded can be generally inferred as those experienced by epiphytes at these sites. The dataloggers were set to record at intervals of 2 h for a period of 12 months and were recollected on a fieldtrip in May 2013. Length of the growing season was calculated as the number of days per year where temperature rose above 5 °C during the day (see Körner 2011 for other definitions). This definition was used as higher plants are understood to need temperatures above 5 °C to grow, mature their seasonal foliage and reproduce (Körner 2003).

Results

High-elevation vascular epiphytes

Three fern species were found growing epiphytically on *Polylepis pepeii* trees at elevations above 4,250 m (Table 1) in all three sites. Two species of *Melpomene*, *M. peruviana* and *M. personata*, were found to elevations above 4,500 m with *M. peruviana* occupying the highest elevation record at c.4,542 m. *Melpomene peruviana* was the more common species to be found at high elevations, being present at all three sites at elevations above 4,500 m. *Melpomene personata* was less frequent at these elevations with only one specimen being found above 4,500 m at site 3, but being found at a lower elevation of c.4,250 m at site 1. Both *Melpomene* species were only found as epiphytes in the study area, although higher elevation records have been found from terrestrial dwelling specimens of the same species (Solomon 1999; Lehnert 2013), meaning these species are 'facultative epiphytes' according to Zotz (2013a, b). *Polypodium chrysoplepis* occupied the lowest elevations

Table 1 List of epiphytic vascular plants and arboreal hemiparasites recorded at elevations above 4,250 m with the highest elevation recorded for each species and details of the specimen voucher

Species	Highest elevation recorded (m)	Voucher
Vascular epiphytes		
<i>Melpomene peruviana</i> (Desv.) A.R. Sm. & R.C. Moran	4,542	Sylvester 1869
<i>Melpomene personata</i> Lehnert	4,527	Sylvester 1867
<i>Polypodium chrysoplepis</i> Hook.	4,288	Sylvester 1585
Arboreal hemiparasite		
<i>Tristerix longebracteatus</i> (Desr.) Barlow & Wiens	4,618	Sylvester 2024

being found to c.4,288 m and was found both epiphytic and terrestrial in the study area and so can also be classed as a 'facultative epiphyte'. All vascular epiphyte species were found to occupy the tree bole or primary branches and were found at heights of 1–2 m from the forest floor. A hemiparasitic member of the family Loranthaceae, *Tristerix longebracteatus*, not considered to be a true epiphyte, occupied the highest elevations being recorded growing on both *P. pepeii* and *Gynoxys cuzcoensis* Cuatrec. (Asteraceae) trees up to 4,618 m. This species generally occupied the outer canopy and was found at heights of 3–8 m from the forest floor.

The elevational position of the treeline was found to be c.4,650 m at all of the sites, but this elevation was only reached, and the highest trees checked for epiphytes, at site 1. The elevation reached at sites 2 and 3 was 4,550 and 4,570 m, respectively, due to difficulties of access to the highest forests.

Site microclimate

There was a distinct dry season from May to November which also coincided with the coldest months of the year (Fig. 2a). Diurnal temperature fluctuations were very pronounced with the coldest days having an average difference of 14.6 °C between the highest and lowest values and the greatest temperature difference of 17.6 °C in the month of August. Site 2 had generally lower temperatures than site 1 (Table 2; Fig. 2a) with a lowest temperature of −5.5 °C reached in the months of August and September. The number of days on which temperatures dropped below 0 °C was also greater for site 2 with 131 days through the months of April–October. In comparison, site 1 only experienced 23 days during the months of June–September where temperatures dropped below 0 °C. The longest frost-free period (i.e. the greatest number of days where temperatures did not

Fig. 2 Minimum (*thin lines*) and maximum (*bold lines*) air temperature (**a**) and relative air humidity (**b**) at sites 1 (*grey*) and 2 (*black*) over the period of 1 year

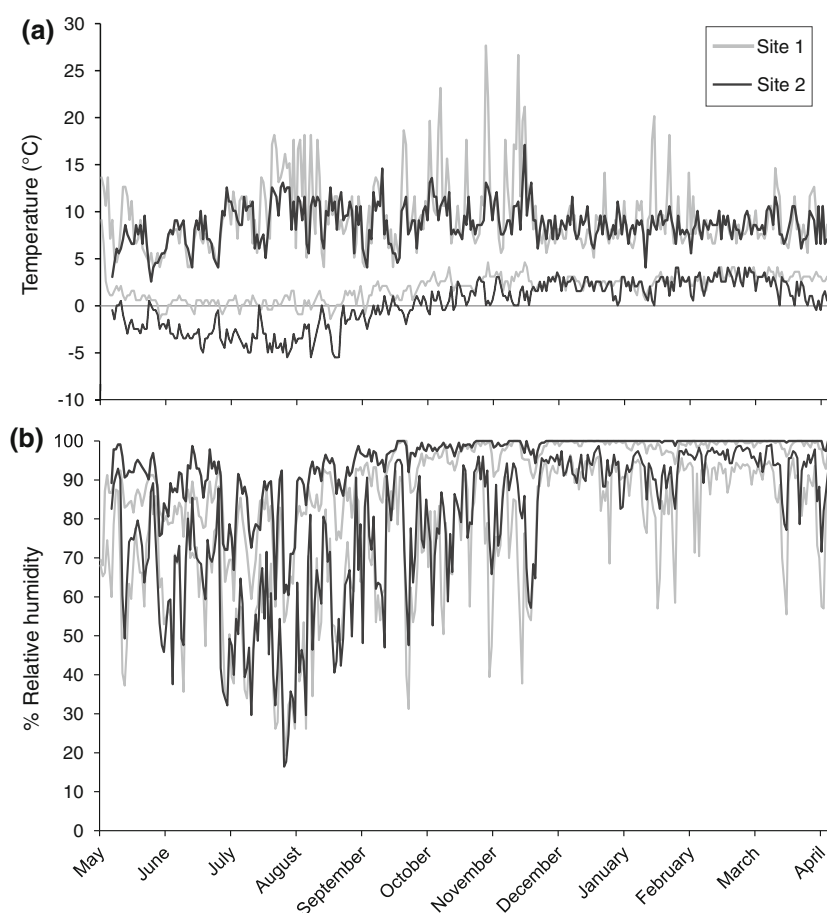


Table 2 Air temperature and relative humidity records from sites 1 and 2

	Site 1	Site 2
Absolute minimum temperature (°C)	−1.4	−5.5
Absolute maximum temperature (°C)	27.7	17.1
Mean daily minimum temperature (°C)	1.9	0.1
Mean daily maximum temperature (°C)	9.5	8.7
Mean daily temperature (°C)	4.2	3.3
Days/year where temperature dropped below 0 °C	23	131
Length of frost-free period (days)	270	168
Growing season (no. of days where temperature rises above 5 °C)	351	352
Absolute minimum relative humidity (%)	14.2	13.4
Mean daily relative humidity (%)	80.9	86.3
Days/year where relative humidity passed 90 %	184	247
Days/year with fog occurrence (relative humidity passed 99 %)	125	178

drop below 0 °C) was documented from site 1 with 270 days from 14th September 2012 till 11th June 2013. Site 2 had a shorter frost-free period spanning 168 days from 25th October 2012 to 11th April 2013. The length of

the growing season, calculated as the number of days where temperature rose above 5 °C, was similar for both sites and was almost year round with 351 days for site 1 and 352 days for site 2. Site 2 had a generally higher relative humidity compared to that of site 1 (Table 2; Fig. 2b) with 247 days where relative humidity reached past 90 % as opposed to 184 for site 1. The daily occurrence of fog, whereby air relative humidity reaches past 99 % on any given day in the year, was also higher in site 2 with 178 days as opposed to 125 days in site 1.

Discussion

Our study documents, to our knowledge, the highest vascular epiphytes and highest arboreal hemiparasites found to date. In the following, we place these records in relation to potential limitations to epiphyte growth at high elevations.

Abiotic constraints on the elevational limits of vascular epiphytes

As our dataloggers were originally intended to measure climatic conditions for the ground vegetation within the

studied forests, we did not situate them exactly where vascular epiphytes were encountered (i.e. on the tree bole and primary branches, 1–2 m from the forest floor), but rather at the tree base. Furthermore, they were placed at slightly higher elevations than the highest epiphyte specimens encountered. Our microclimatic data may, thus, not reflect actual conditions at the highest localities where vascular epiphytes were found. Other studies have found higher sections of trees to experience more pronounced fluctuations in temperature and humidity and be generally drier compared with tree bases (Parker 1995; Karger et al. 2012). Therefore, it is likely that the conditions experienced by the species in our study region are more extreme than those that are presented here. Despite these limitations, our data provide approximate measurements of the climatic conditions at the growth sites of the epiphytes and are probably the most reliable data obtained to date at the upper limit of tropical vascular epiphytism.

Previous studies have placed temperature and, in particular, the occurrence of frost as the principal limiting factors on the elevational distribution of vascular epiphytes (Krömer et al. 2005 and references therein). The *Melpomene* species demonstrate a great physiological tolerance to low temperatures, experiencing up to 131 days of freezing temperatures per year. However, if we consider the growing season for ferns at these elevations as being days per year in which temperatures rise above 5 °C (Körner 2003), then each fern has almost a year-round growing season. These temperatures are similar to those experienced in *Polylepis pepeii* forests at 4,000 m in the Bolivian Andes (Kessler and Hohnwald 1998; Krömer et al. 2005) and do actually appear fairly amenable for fern epiphyte survival if compared with other studies outside of the Andes. Bhattarai et al. (2004) found the growing season for epiphytic ferns in the Himalayas to be significantly shorter with c.120 days/year in comparison with >351 days/year in the Cordillera Vilcabamba sites. This difference reflects the stronger climatic seasonality of the Himalayas (c. 28°N) as compared to our study area (13°S).

If we compare this temperature data with ecological data on temperate vascular epiphytes from higher latitudes, specifically *Polypodium vulgare* at 1,300 m in the Swiss Alps (c. 47°N; Zotz 2002), it can be seen that the temperatures that *Melpomene* experience at these elevations are not that low compared with what *P. vulgare* has to endure. The mean yearly absolute minimum temperature, taken from 36 years of temperature recording, was −16.4 °C, much lower than the −5.5 °C absolute minimum experienced in the study area. The physiological tolerance of *P. vulgare* to cold temperatures may be much greater than the *Melpomene* species studied here, although there are other variables that should be compared (i.e. number of frost days, length of growing season, annual mean minimum temperature) to assess the cold limits of vascular epiphyte life.

We present the first data on air relative humidity recorded from sites where temperate vascular epiphyte growth has been documented. Both sites 1 and 2 experienced a high relative humidity with over half the year having days where relative humidity rose above 90 %. Interestingly, no vascular epiphytes have been noted from *Polylepis* forests above 3,800 m in the neighbouring Cordillera Vilcanota, which experience similar temperature regimes to the current sites studied (Sylvester et al. *unpubl. data*). Therefore, it could be conjectured that the comparatively drier climates of these areas (Toivonen et al. 2011) likely inhibit the establishment and survival of vascular epiphytes that are wholly dependent on precipitation and atmospheric humidity for their water supply.

Biotic constraints on the elevational limits of vascular epiphytes

It comes as little surprise that the grammitid fern genus *Melpomene* holds the world record for the highest elevation vascular epiphyte. Previous studies have already found this genus to occupy very high elevations in the Andes (Krömer et al. 2005; Lehnert 2013). What special physiological characteristics pertain to the *Melpomene* species that allow them to grow at these elevations remains a question that awaits experimental analysis.

Habitat availability appears to be one of the main constraints on the elevational limit for growth of the two *Melpomene* species in the Cordillera Vilcabamba. The species definitely did not seem at their ecophysiological limits and were common in all the high-elevation forests studied with all populations found to be reproducing (although the viability of the spores would need to be tested to verify this claim). This implies that these high-elevation populations are source populations and not sink populations, as suggested by Bhattarai et al. (2004) who found ferns in the alpine environment to be mainly sink populations of sub-alpine species which can barely tolerate the harsh and stressful open alpine habitat. At both sites 2 and 3, where *Melpomene* species were found epiphytic in the highest trees encountered, the forests extended to even higher elevations than those that were possible to reach in the present study. Therefore, it is plausible that the upper elevational limits on vascular epiphyte growth may be even higher than presently documented.

High-elevation arboreal hemiparasites

This study also gives a new elevational world record for arboreal hemiparasites with *Tristerix longibracteatus* being found at c. 4,620 m. The species was a common constituent of the *Polylepis pepeii* forests at site 1, but its absence in sites 2 and 3 could relate to either ecophysiological limitations or

habitat preferentiality of their avian dispersers. Site 1 had a more amenable climate compared to site 2 with fewer days of frost occurrence and air temperatures generally warmer that is likely to be more favourable habitat for arboreal hemiparasites and their associated avian dispersers. However, with no data collected on avifaunal composition and fruit dispersal specificities from the sites, we cannot disentangle the importance of ecophysiological limitations and avian dispersers in shaping the elevational limits of arboreal hemiparasites.

Conclusion

This is the first study to document vascular epiphytes, arboreal hemiparasites and their abiotic conditions from elevations over 4,000 m. A number of factors lend themselves to the Cordillera Vilcabamba holding the world record for high-elevation vascular epiphytes and arboreal hemiparasites; a combination of (a) humid climate, caused by updrafts of moisture laden air from the Amazon, and (b) presence of high-elevation forests, create the ideal niche for survival at elevations previously undocumented. Temperature, substrate and water availability are all conjectured as being important in determining the upper hard boundary of vascular epiphyte survival, whilst the elevational limits of arboreal hemiparasites could also be linked to the availability of avian dispersers. Further research is required to resolve which of these factors takes precedence in determining these elevational limits.

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